

Girdling Vascular Bundles in Dicotyledon Flowers

by

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Summary

For more than 35 years, girdling vascular bundles have been known to occur in the flowers of species belonging to nine families of dicotyledons. Further families are now added to the list, bringing the total to twenty. The occurrence of girdling bundles does not appear to have any special taxonomic or phylogenetic significance. Vascular patterns with girdling bundles are illustrated for members of eleven families.

The purpose of this paper is to draw attention to a phenomenon which is more widespread among dicotyledons than has hitherto been realized, namely, the occurrence within the floral receptacle of a horizontal girdling vascular bundle which connects the vascular bundles supplying the perianth members.

The term "girdling vascular bundle" was used by Saunders (1939) to describe such lateral interconnections in species belonging to the Cistaceae, Combretaceae, Lythraceae, Melastomataceae and Onagraceae. In four other families (Campanulaceae, Hydrocaryaceae, Rubiaceae and Valerianaceae) she mentioned lateral connections but did not refer to them as girdles. To judge from her books, and from the references quoted therein, Saunders (1939) must have looked at representatives of at least 168 families of dicotyledons. Having examined representatives of more than 150 families myself, I have been able to add a further eleven to the list of those with girdling bundles. Three of these (Leguminosae, Tropaeolaceae and Violaceae) have already been briefly described (Sporne, 1974). The other eight families are Begoniaceae, Caricaceae, Ericaceae, Flacourtiaceae, Gentianaceae, Loasaceae, Stylidiaceae and Tiliaceae, which bring to twenty the total number of families in which this phenomenon has been recorded.

As will subsequently become apparent, some distinction needs to be made between those girdles in which both the sepals and the petals are involved and those in which the petals alone are involved or the sepals alone. It is proposed to call the first type "composite girdles" and the second type either "simple corolla girdles" or "simple calyx girdles", respectively.

Vascular connections between the sepals and the petals in *Campanula* and *Lobelia* were mentioned by Henslow (1888), but the details of his description were not correct. Thus, in *Campanula medium* L., he stated that the vascular bundle intended for a sepal branches before reaching it and sends off two cords, one for each petal alternating with it, "so that each petal receives two cords, one from each adjacent sepal — a most unusual condition of things, for petals have almost invariably their own cords issuing from the pedicel." If this description were correct it would, indeed, be unusual, for I know of only one example of a flower whose petals derive their entire vascular supply from that of the sepals, viz. *Viola* (Sporne, 1974, fig. 52C).

Plate 1 is a photograph, taken in the late Autumn, of an old flower of *Campanula carpatica* Jacq. At this time in the year, the soft tissues of the flower have rotted away, leaving just the vascular skeleton. The crown-like composite girdle is clearly visible. Fig. 1 is a stylized vertical projection of the vascular system in *Campanula rotundifolia* L., (omitting the supply to the gynoeceum). Three

vascular bundles enter the base of the flower and branch, somewhat irregularly, in the wall of the inferior ovary, until near the top there are ten trunk bundles. Of these, five are on the sepal radii and, giving rise to the five stamen bundles (A),

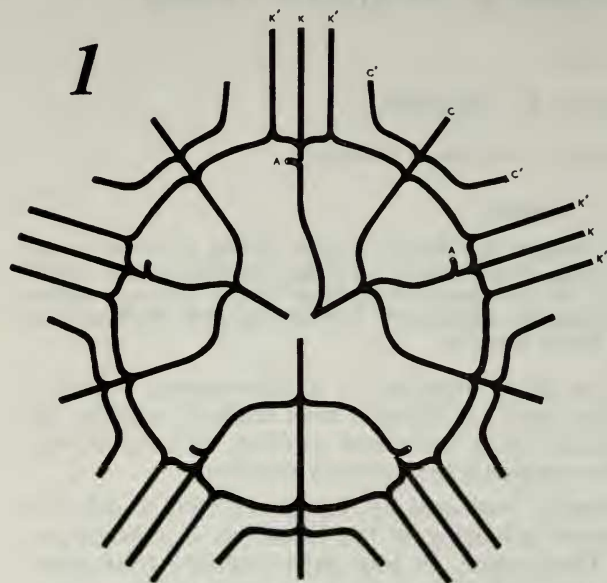


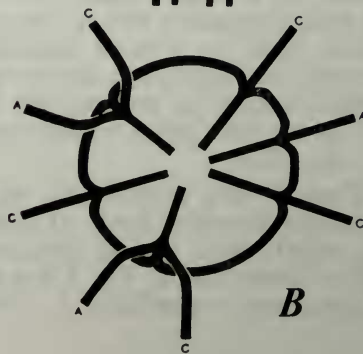
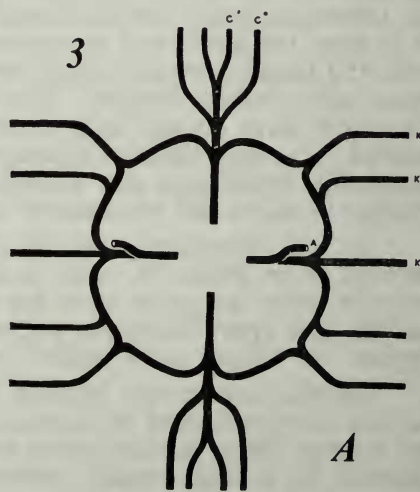
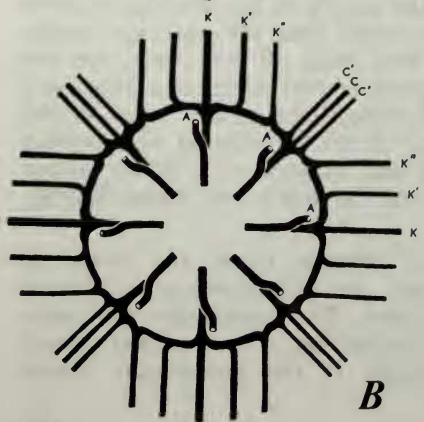
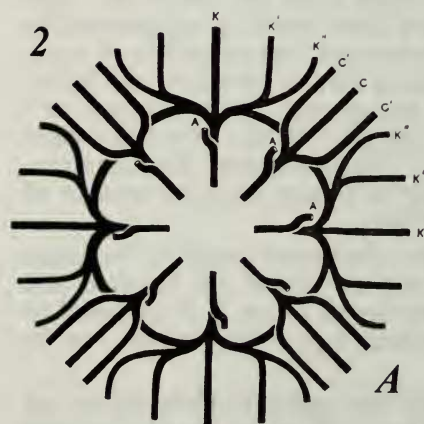
Fig. 1. *Campanula rotundifolia* L.

Fig. 2. A, *Fuchsia fulgens* Moç. and Sessé ex DC.

B, *Epilobium angustifolium* L.

Fig. 3. A, *Circaea lutetiana* L.

B, *Valeriana officinalis* L.



are continuous with the sepal mid-ribs (K). The other five trunk bundles are on the petal radii and continue into the petals, giving both the petal mid-rib (C) and the petal laterals (C'). Before the petal supply becomes distinct, however, all ten trunk bundles become connected by a horizontal girdle. It is from this girdle, and not from the sepal mid-rib, that the sepal laterals (K') have their origin. A similar composite girdling bundle has been figured by Mabberley (1973) for *Lobelia stricklandiae* Gilliland.

Fig. 2 illustrates the vascular system of two members of the Onagraceae, namely, *Fuchsia fulgens* Moç. and Sessé ex DC. and *Epilobium angustifolium* L. (Note that here, as in all the other illustrations, the vascular supply to the ovules and to the style is omitted.) In each of these two genera, there are eight trunk bundles in the wall of the inferior ovary, and a stamen bundle arises as a branch from each. They then become connected by a horizontal girdle which, in *Fuchsia*, is below the level of origin of the sepal and petal lateral bundles. In *Epilobium*, however, these lateral bundles have their origin in the girdle itself. *Circaea lutetiana* L. (Fig. 3A) also belongs to the Onagraceae, but has a much smaller flower than either *Fuchsia fulgens* or *Epilobium angustifolium*, yet it too has a horizontal girdle. There are four trunk bundles in the wall of the ovary, corresponding to the two sepals and the two petals, respectively. Each sepal receives five bundles, of which the laterals (K' and K'') are derived from the girdle. The petal laterals (C'') are, however, independent of it, as in *Fuchsia fulgens*.

Valeriana officinalis L. (Fig. 3B), also has a very small flower. Its calyx is represented merely by about twelve curled teeth, which receive no vascular supply at all. Six trunk bundles run up in the wall of the inferior ovary; two of them fork, to provide the total of eight needed for the five petals and the three stamens, and then a horizontal girdle is formed, for which the term "simple corolla girdle" is appropriate.

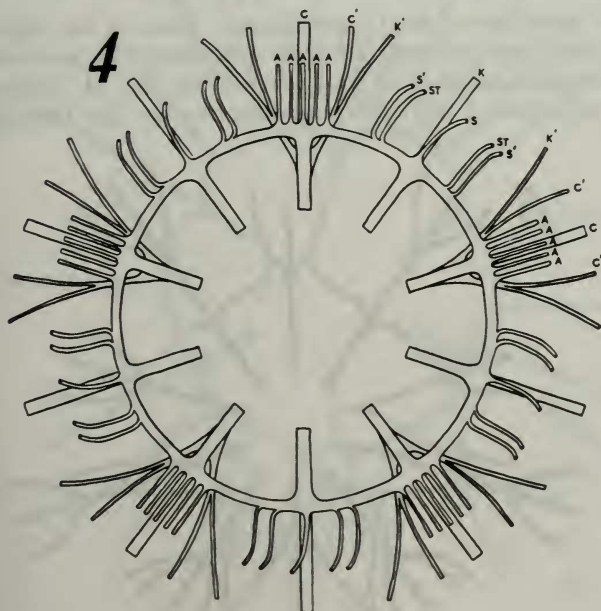


Fig. 4. *Loasa vulcanica* André.

Plate 2 illustrates the importance of clearing techniques when studying floral vascular systems. A horizontal slice through the apex of the inferior ovary of *Loasa vulcanica* André, was boiled for a few seconds in lactic acid (Sporne, 1948) and was then photographed by transmitted light. The vascular bundles show up as a silhouette, in which the horizontal composite girdle is clearly visible. A structure as complex as this would have been very difficult to envisage from a study of a series of microtome sections. Fig. 4 is a diagrammatic interpretation, based on several slices cut at slightly different levels. Opposite each

of the five sepals there is a petaloid scale, receiving three vascular bundles (S and S') and inside each scale there are two staminodes (ST). The stamens (A) are in groups opposite the five petals. The sepal lateral (K') and the adjacent petal lateral (C') arise conjointly from the petal trunk bundle at a level slightly below that of the girdle.

Fig. 5 shows part of the receptacular vascular system in *Mentzelia lindleyi* Torr. & Gray, which belongs to the same family as *Loasa*, namely the Loasaceae.

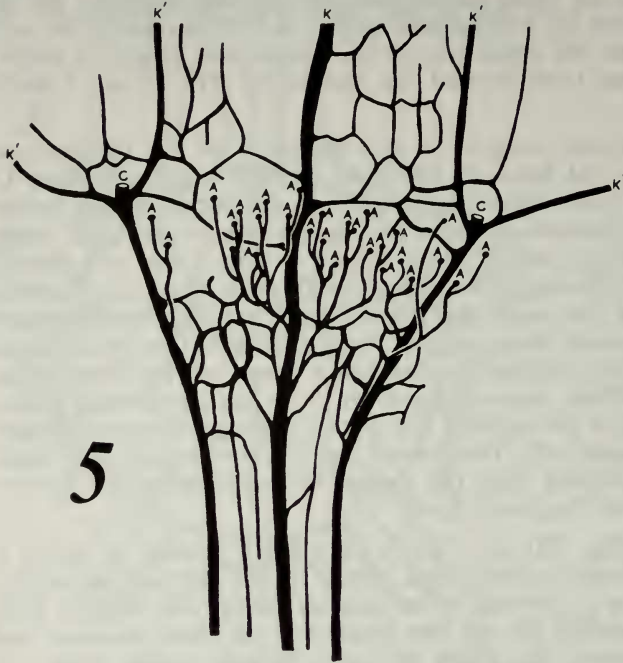


Fig. 5. *Mentzelia lindleyi* Torr. & Gray.

A portion of the receptacle was opened out flat and viewed from inside, after being cleared in lactic acid. The vascular system is strikingly different from that of *Loasa* for, instead of a single girdling bundle, there is an anastomosing system connecting the sepal and petal trunk bundles and from it the stamens receive their vascular supply. A similar arrangement occurs in *Mentzelia gronoviiifolia* Fisch. & Mey. Clearly, it would be unwise to generalize, on the basis of one genus within a family, about the occurrence of girdling bundles, for one can scarcely describe *Mentzelia* as having a girdle.

This is true also of various members of the Cucurbitaceae. Thus, in the edible cucumber, *Cucumis sativus* L., there are ten trunk bundles connected by a network of smaller bundles, while the vascular network of *Luffa cylindrica* (L.) M. Roem., is even more noticeable, especially after it has been retted to produce the familiar bathroom loofah. The Cucurbitaceae can scarcely be said to have a vascular girdle even though, from a physiological point of view, the vascular connections may be directly comparable.

Stylidium graminifolium Sw. ex DC, belonging to the Stylidiaceae, raises a similar problem. Running up in the wall of the inferior ovary, there are ten trunk bundles (Fig. 6), some of which are connected by horizontal bundles, while others are connected only by obliquely running bundles. Perhaps *Stylidium* should be described as having only a partial girdle.

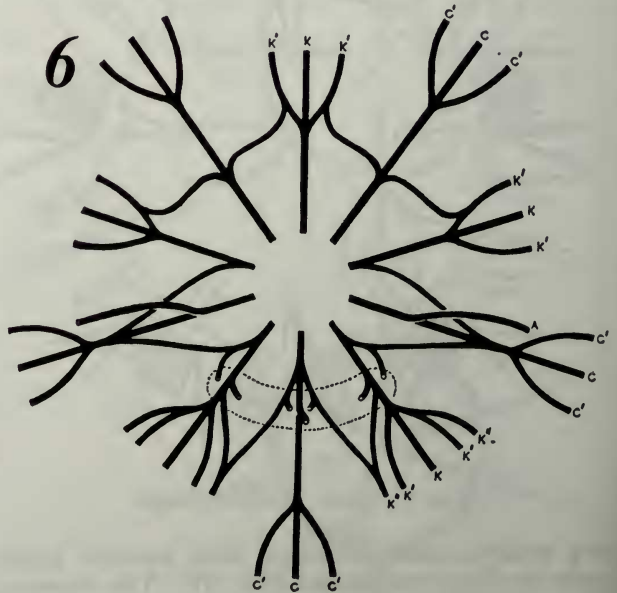


Fig. 6. *Stylidium graminifolium* Sw. ex DC. (The broken line represents a nectary.)

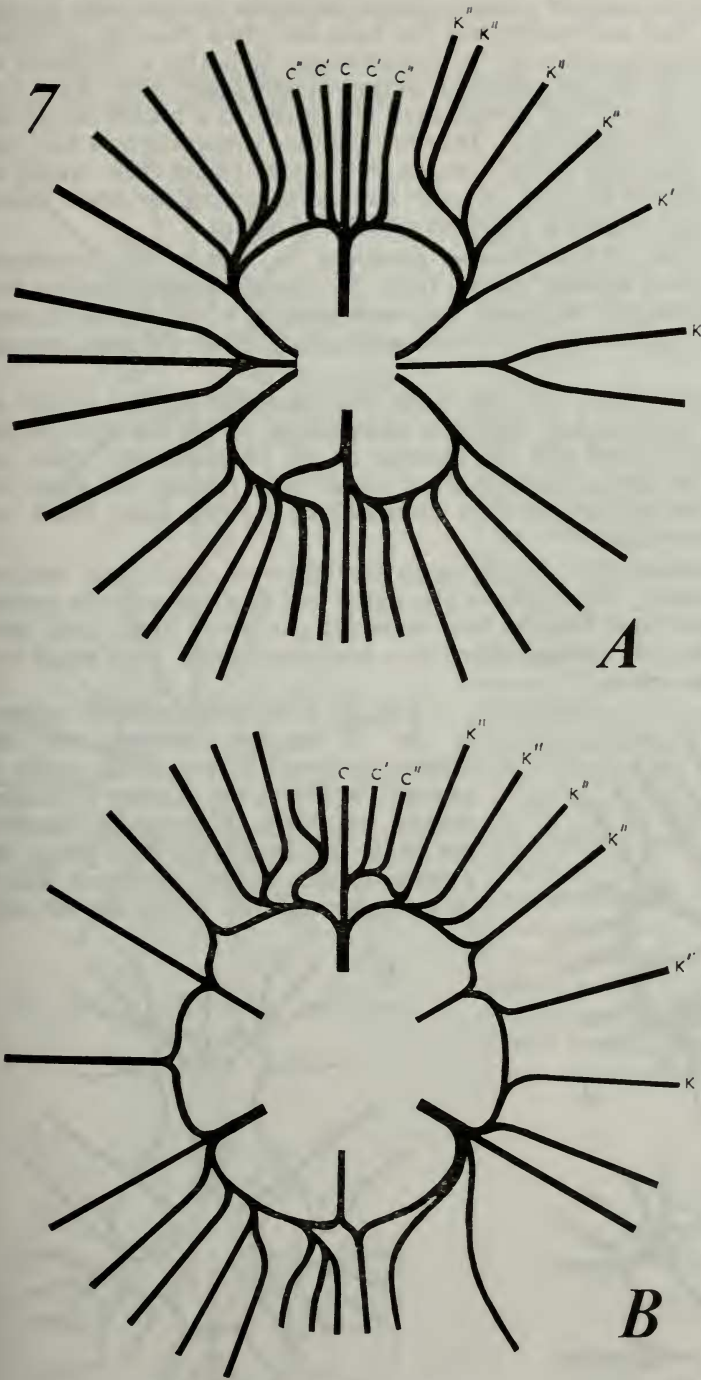


Fig. 7. *Begonia evansiana* Andr. A, staminate flower. B, pistillate flower.

The examples quoted so far have all been of hermaphrodite flowers. *Begonia evansiana* Andr. has unisexual flowers, and there is a well developed horizontal girdle in the pistillate flower, but only a partial one in the staminate flower. In each, there are two sepals and two petals. Fig 7A shows how, in the staminate flower, there are eight trunk bundles of which two lead directly into the sepal mid-ribs, while the remaining six become involved in two semi-circular partial girdles opposite the petals. The pistillate flower (Fig. 7B) has six trunk bundles in the wall of the inferior ovary which are connected by a complete horizontal composite girdle, from which petal laterals as well as sepal laterals originate.

Girdling bundles are more likely to occur in flowers where the perianth members are whorled, or even connate, rather than in those with spirally arranged

perianth members. It is not surprising, therefore, that many examples of girdling bundles are found in flowers with inferior ovaries, where adnation, as well as connation may have occurred as a result of "intercalary concrescence" (a term suggested by Stebbins, 1974, which avoids the ambiguities of "fusion"). However, there are

also several families with superior ovaries whose perianths receive their supply from girdling bundles. Such an arrangement has been described (Sporne, 1974) for *Phaseolus*, in the papilionate section of the Leguminosae. It is also to be found in *Cassia floribunda* Cav., in the caesalpinoid section of the family (Fig. 8A). Ten trunk bundles enter the base of the flower, each giving rise to a branch supplying either a stamen (A) or a staminode (ST). They then become connected by a horizontal girdle, from which the sepal lateral bundles (K' and K'') have their origin. In passing, it should be noticed that the vascular bundles supplying the three lowermost stamens are peculiar in having a hollow cylinder of xylem.

Among the Ericaceae, *Rhododendron ponticum* L., has a well developed composite girdle. Ten trunk bundles radiate from the central cylinder. As they run horizontally in the disc-shaped receptacle, they each give off a stamen bundle and then all ten bundles are united by a horizontal girdle, from which the sepal laterals have their origin.

Fig. 9 (taken from Sporne, 1974, fig. 52A) illustrates the vascular system in *Tropaeolum minus* L. (The stamen supply is independent of the perianth supply and has, therefore, been omitted.) In this member of the Tropaeolaceae, there are ten trunk bundles in the base of the flower, of which three run the full length of the spur and back again. All ten are then connected by a girdle, from which the sepal laterals have their origin.

In *Sparmannia africana* L. f., belonging to the Tiliaceae, eight trunk bundles enter the base of the flower, four opposite the sepals and four opposite the petals. Despite the fact that the sepal bundles turn outwards at a much lower level than do the petal bundles, they all become united by a horizontal girdle, from which the sepal laterals have their origin.

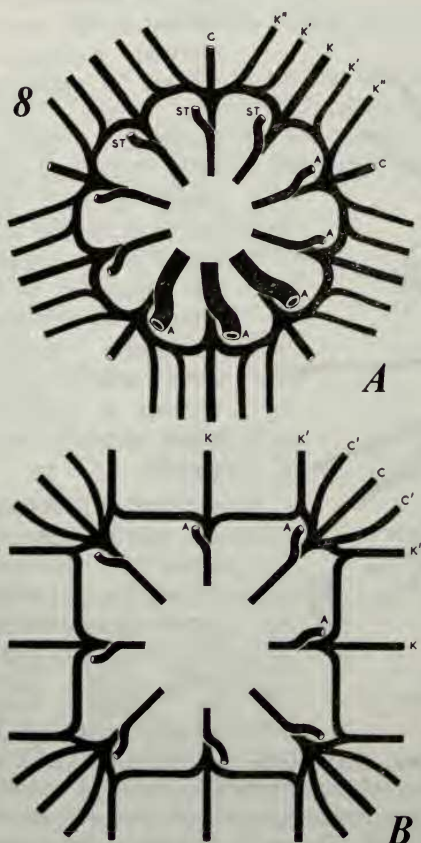


Fig. 8B is of *Heterocentron roseum* A. Br. & Bouché, belonging to the Melastomataceae. Although the ovary is superior, it lies at the bottom of a cup-shaped receptacle. Eight trunk bundles run up in this receptacle, each giving off a stamen trace before becoming linked by a composite girdle. This is not the only

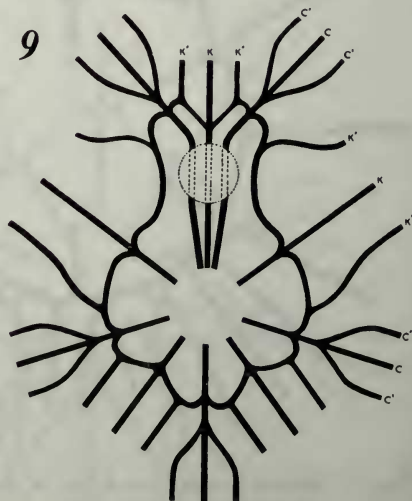


Fig. 8. A, *Cassia floribunda* Cav.
B, *Heterocentron roseum* A. Br. and Bouché.

Fig. 9. *Tropaeolum minus* L. (The broken lines represent the spur.)

link, however, for there are some anastomosing bundles in addition, below the level of the girdle.

Passiflora quadrangularis L. has a similar anastomosing network, but none of the connections is sufficiently large to justify the term "girdle". This arrangement is therefore equivalent to that in the Cucurbitaceae. Neither Passifloraceae nor Cucurbitaceae qualify for inclusion among those families with girdling bundles, as defined in this paper.

Fig. 10 illustrates two genera belonging to the Gentianaceae, one of which has a simple calyx girdle, while the other is completely without any lateral connections. The flower of *Blackstonia perfoliata* (L.) Huds., illustrated in Fig. 10A, was one with eight sepals. Each received a mid-rib (K) and lateral veins (K'); and each pair of adjacent laterals was joined by a short bridging bundle, so as to produce a "zig-zag" girdle. *Chironia linoides* L. (Fig. 10B) has pentamerous flowers in which the sepal supplies are completely independent of each other. *Centaurium minus* Moench, also belonging to the Gentianaceae, is variable in that bridges between adjacent sepal laterals are sometimes present and sometimes absent.

In *Phyllobotryon spathulatum* Muell. Arg., belonging to the Flacourtiaceae, the vascular supply to the three sepals is completely separate from that to the three petals, yet there are lateral connections in each system. Fig. 11A shows the calyx system, in which lateral connections form a partial girdle. Fig. 11B shows the corolla system, in which there are merely a few random interconnections.

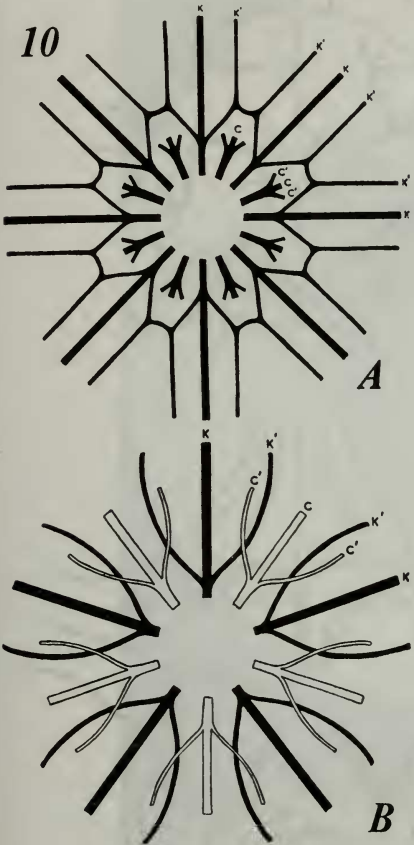


Fig. 10. A, *Blackstonia perfoliata* (L.) Huds.
B, *Chironia linoides* L.

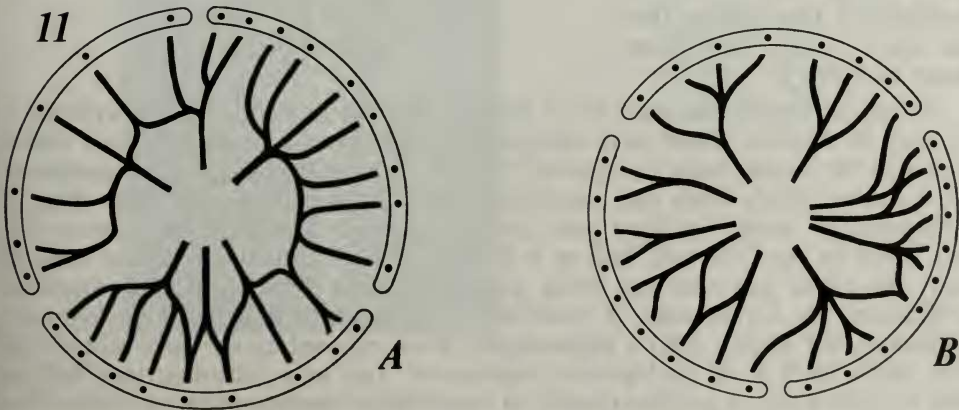


Fig. 11. *Phyllobotryon spathulatum* Muell. Arg. A, calyx. B, corolla.

The most remarkable vascular system that I have seen is that of *Carica papaya* L., illustrated in Fig. 12. The flowers are pentamerous and unisexual; and the perianth members derive all their vascular supply from five trunk bundles. However, the way in which this happens is in the staminate flowers is strikingly different from that in the pistillate flowers. Fig. 12A illustrates the vascular pattern of a staminate flower, in which there is a complete and simple calyx girdle, each sepal receiving a midrib (K) and two lateral veins (K'). The trunk bundle to each petal has its origin, not independently from the central cylinder, but runs for a short distance conjointly with a sepal trunk bundle; then, on becoming separate, it moves laterally on to a different radius. In the pistillate flower, illustrated in Fig. 12B, there is some variability, but mostly the petal trunk bundles arise conjointly with sepal trunk bundles, as in the staminate flower. However, the sepals receive many veins, the number varying from sepal to sepal, and only a partial girdle is formed. In passing, attention must be drawn to the stamen supply in the staminate flowers. The particular flower illustrated in Fig. 12A had five trunk bundles, which became connected by a partial girdle from which the ten stamen bundles had their origin (but the exact details vary from flower to flower).

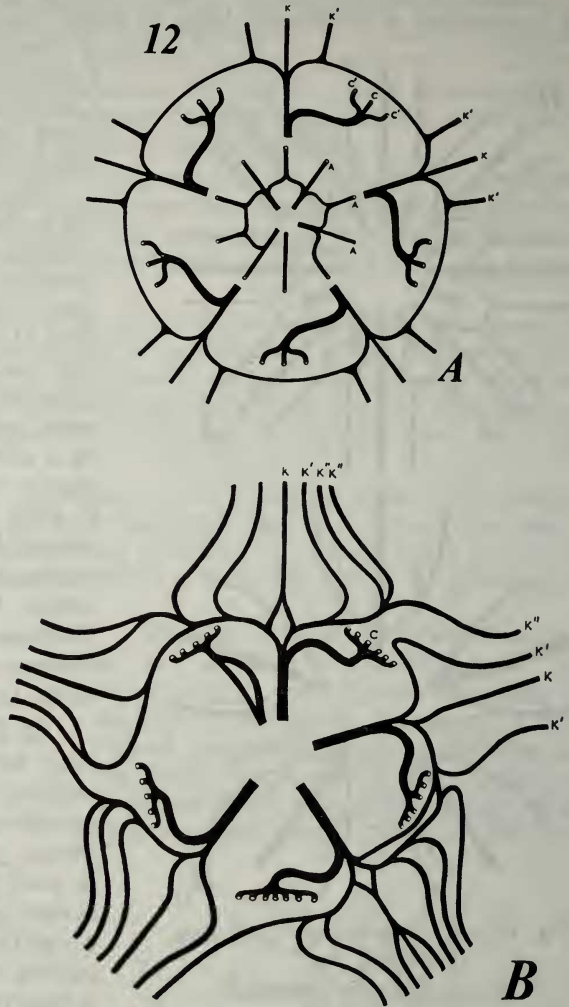


Fig. 12. *Carica papaya* L.
A, staminate flower.
B, pistillate flower.

What the significance may be of girdling bundles in floral vascular systems is not easy to discern. There have always been two schools of thought, one which holds that the course taken by vascular bundles is of great phylogenetic significance and the other which holds that vascular bundles develop where and when there is a physiological need. To those who hold the former view, Professor Corner has been heard to say "Go and look at a loofah", for of course it would be hard to justify the claim that each and every strand in such a network is of phylogenetic significance. Yet a reticulum, if described as such, might well be of phylogenetic significance, for it may fulfil a physiological need imposed by the large size of the fruit, which itself is of phylogenetic significance. Just as a reticulum may fulfil a need, so indeed may a girdling bundle, in providing alternative paths of conduction, analogous to closed vascular networks in stems.

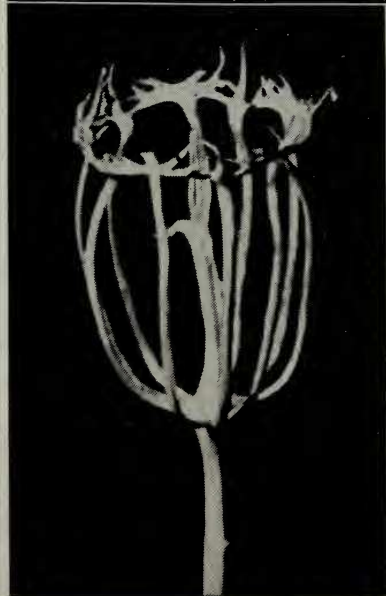


Plate 1. (above) *Loasa vulcanica* André., showing composite girdle. $\times 20$.

Plate 2. (below) *Campanula carpatICA* Jacq. Vascular skeleton of flower. $\times 3$.